FINAL REPORT FOR:

US FOREST SERVICE
ROCKY MOUNTAIN RESEARCH STATION CONTRACT:
05-JV-11221659-169

"A SYNTHESIS OF THE BIOLOGY OF JAPANESE WHITE-SPOTTED CHARR (*SALVELINUS LEUCOMAENIS*) AND NORTH AMERICAN BULL TROUT (*S. CONFLUENTUS*) WITH IMPLICATIONS FOR CONSERVATION AND RESEARCH NEEDS"

PREPARED BY

COLDEN V. BAXTER
DEPARTMENT OF BIOLOGICAL SCIENCES
IDAHO STATE UNIVERSITY
POCATELLO, ID 83209-8007

THESIS/REPORTS
BAXTER, C.V.

FINAL REPORT FOR:

US FOREST SERVICE

ROCKY MOUNTAIN RESEARCH STATION CONTRACT:

05-JV-11221659-169

"A SYNTHESIS OF THE BIOLOGY OF JAPANESE WHITE-SPOTTED CHARR (*SALVELINUS LEUCOMAENIS*) AND NORTH AMERICAN BULL TROUT (*S. CONFLUENTUS*) WITH IMPLICATIONS FOR CONSERVATION AND RESEARCH NEEDS"

PREPARED BY

COLDEN V. BAXTER

DEPARTMENT OF BIOLOGICAL SCIENCES

IDAHO STATE UNIVERSITY

POCATELLO, ID 83209-8007

ECOLOGY AND CONSERVATION OF DOLLY VARDEN, WHITE-SPOTTED CHAR, AND BULL TROUT

Authors (in alphabetical order):

Colden Baxter, Asst. Professor, Idaho State University, Pocatello, Idaho

Jason Dunham, Research Fish Ecologist, USGS, Corvallis, Oregon

Kurt Fausch, Professor, Colorado State University, Fort Collins, Colorado

Wade Fredenberg, U.S. Fish and Wildlife Service, Creston, Montana

Satoshi Kitano, Environmental Conservation Institute, Nagano, Japan

Itsuro Koizumi, Postdoctoral Researcher, University of Helsinki, Finland

Kentaro Morita, Ocean Research Institute, University of Tokyo, Japan

Tomoyura Nakamura, National Research Institute of Fisheries Science, Nikko, Japan

Bruce Rieman, Fisheries Research Biologist, USFS, Boise, Idaho

Ksenia Savvaitova, Professor, Moscow State University, Russia

Jack Stanford, Professor, Flathead Lake Biological Station, University of Montana

Shoichiro Yamamoto, National Research Institute of Fisheries Science, Nikko, Japan

To be submitted to: *Fisheries*

Introduction[1]

Most research on salmonine fishes has focused on the genera *Oncorhynchus* (e.g., Pacific salmon and rainbow trout) and *Salmo* (e.g., Atlantic salmon and brown trout). Within the genus *Salvelinus*, work has focused mostly on Arctic char (*S. alpinus*), lake trout (*S. namaycush*), and brook trout (*S. fontinalis*). Though research on these species has provided a broad foundation for understanding the biology, ecology, and conservation biology of salmonines, even within this well-studied group there are gaps in understanding and uncertainties that pose significant problems for management and conservation. For example there are several species of *Salvelinus* or chars that are imperiled throughout substantial portions of their native ranges, but about which less is known. We focus this paper on the biology and conservation of three chars: Dolly Varden char (*S. malma*), white-spotted char (*S. leucomaenis*), and bull trout (*S. confluentus*). We chose to consider these species together because they share a common geography (Fig. 1) and evolutionary history, and provide an instructive comparison of the conservation problems and uncertainties associated with management of native chars in North America and Asia. Our specific objectives here are to 1) provide a brief overview of what is known of the evolution and ecology of these three species; 2) compare and contrast conservation issues within and among the species, and 3) provide our view of priorities for future research and conservation efforts.

---

[1] Insert disclaimer here for why we use 'char' (AFS convention) while the rest of the world uses "charr"

Biogeography and evolutionary history

Dolly Varden, white-spotted char, and bull trout are distributed across the North Pacific rim (Fig. 1). The most widespread species is Dolly Varden, whose range extends from Puget Sound in Washington State, U.S.A., north to the Alaska Peninsula and far eastern Asia, including northern Siberia and neighboring islands, south to Hokkaido, the northernmost island of the Japanese archipelago (Armstrong and Morrow 1980). White-spotted char is distributed from Honshu (the main island of Japan) north to the Navarin Cape, Russia (Savvaitova 1980; Kawanabe 1989), on the Asian side of the North Pacific coast. Bull trout occupies coastal and inland drainages from southern Alaska to Oregon, but have been extirpated from the southernmost extent of their historic range in northern California, U.S.A. (Cavender 1978; Haas and McPhail 1991). Both white-spotted char and bull trout overlap with Dolly Varden in the northern portions of their respective ranges.

Recent evidence indicates these three chars share a common evolutionary history. Allozyme, nuclear DNA, mitochondrial DNA (mtDNA) analyses all revealed two sister groups within *Salvelinus*: white-spotted char - bull trout and Dolly Varden - Arctic char (Crane et al. 1994; Phillips et al. 1999; Crespi and Fulton 2003). However, a recent study demonstrated that Dolly Varden and Arctic char do not form two monophyletic groups (Brunner et al. 2001), indicating that the taxonomic status of *S. malma* - *S. alpinus* species complex is still questionable. Historical introgressive hybridization has been reported between bull trout and Dolly Varden in populations that are both currently sympatric and allopatric (Taylor 2004), and between white-spotted char and Dolly Varden (Radchenko 2004; Yamamoto et al. 2006). Dolly Varden, therefore, is

introgressed from two other *Salvelinus* species on both north-western American and Asian sides of the Pacific. Evolutionary patterns within Dolly Varden, white-spotted char, and bull trout are distinctive for each species, both in terms of described subspecies and morphological variability.

Across the North Pacific rim, four subspecies of Dolly Varden are recognized (Fig. 2): the northern Dolly Varden *S. malma malma* (Walbaum), the southern Asian Dolly Varden *S. m. krascheninnikovi* (Taranetz), the southern American Dolly Varden *S. m. lordi* (Günther), and the Miyabe char *S. m. miyabei* (Oshima). Chromosome and mtDNA data identified three phylogenetic groups, whose geographic distributions correspond to three Dolly Varden subspecies: *S. m. malma, S. m. krascheninnikovi,* and *S. m. lordi* (Phillips et al. 1999; Oleinik et al. 2005). Miyabe char inhabits only Lake Shikaribetsu, Hokkaido, Japan, which has been isolated historically due to volcanic activity. Miyabe char also has unique morphological characteristics in gill raker counts, pectoral fin length, the number of scales along the lateral line and the muscle color compared to other conspecific populations (Maekawa 1984).

White-spotted char is presently separated into four subspecies based on zoogeographic patterns and morphological characteristics: *S. leucomaenis leucomaenis* (Pallas), *S. l. japonicus* (Oshima), *S. l. pluvius* (Hilgendorf), and *S. l. imbrius* (Jordan et McGregor). Roughly, populations north of Honshu Island, including Hokkaido Island, Japan, and Sakhalin Island and Kamchatka Peninsula, Russia, are classified as *S. l. leucomaenis.* They are characterized by large white spots (Fig. 3). The other three subspecies are endemic to Honshu Island, Japan, each with distinctive coloration (Fig. 3). However, a recent phylogeographic study has shown that the current subspecies

designations of white-spotted char are not compatible with lineages identified with mtDNA markers (Yamamoto et al. 2004). Consequently, the taxonomy *S. leucomainis* remains in question.

At present, no subspecies of bull trout has been proposed, but the species itself was not formally described until relatively recently (Cavender 1978; Haas and McPhail 1991). Within bull trout, multiple lines of evidence suggest at least two major evolutionarily distinct units just below the species level in western North America: coastal and interior bull trout (e.g. Taylor et al. 1999; Taylor and Costello 2006), with further subdivision proposed by other authors (Leary et al. 1993; Spruell et al. 2003). As with subspecies in Dolly Varden, these evolutionary groups within bull trout are associated with patterns of historical hydrographic connectivity (i.e., by the Coastal-Cascade Mountain Crest) across the geographic range of *S. confluentus*. Like white-spotted char, there is considerable variability in coloration among populations of bull trout (Fig. 4) but it is unknown if variation of evolutionary significance occurs.

Diversity of life history types

Around the Pacific Rim, Dolly Varden, white-spotted char, and bull trout each inhabit a broad array of habitats that may present unique physiological challenges and patterns of resource availability, as well as distinct communities that constrain their interactions with other species. This heterogeneity may influence patterns of resource polymorphisms and life history variation observed in these species at a variety of scales (e.g., Smith and Skúlason 1996). Geographic variability in climate, particularly temperature, is believed to be a major driver of phenotypic variation within these chars (Nakano et al. 1996). The

geographic distribution of species that may interact strongly with these native chars is also likely important. Within individual river networks key factors include local variability in thermal and flow regimes; the presence of lakes, reservoirs, and marine habitats; and connectivity among different habitats. Given the broad range of habitat conditions and communities occupied by each species, the extent of intra-specific variation in life history observed is not surprising. Past work has focused on three major facets of life history variation: 1) age and growth, and reproduction, 2) trophic ecology and 4) movement.

Age, growth, and reproduction

Bull trout reportedly first mature between 5 and 7 years of age, white spotted char between 2 and 7 years, and Dolly Varden between 1 and 7. Maximum life spans of these species may exceed 10-15 years or longer. Rapid growth is often associated with movement into more productive environments, including the opportunity for piscivory. Dolly Varden, white-spotted char and bull trout may reach maturity at sizes ranging from <8 to >70 cm depending on growth environments and differential selective pressure on reproduction by males and females (e.g., Jonsson and Jonsson 1993). Migratory individuals which may move from natal tributary streams into rivers, lakes, and the ocean occur in each species and tend to mature at the largest sizes while stream resident individuals mature at very small sizes (Koizumi and Maekawa 2004).

The timing and frequency of spawning can be highly variable. For example, in bull trout, spawning in inland habitats with colder winters may be initiated by late August whereas in systems with warmer winter climates, spawning may occur several weeks

later. Spawning in white spotted char and bull trout is believed to be restricted entirely to stream environments, but wholly lake resident Dolly Varden have been reported from Alaska and the Kamchatka peninsula (Armstrong and Morrow 1980). All species are iteroparous, although mortality associated with spawning can be substantial (>50%).

Trophic ecology

The striking trophic polymorphisms observed in Arctic char (e.g. Jonsson et al. 1988) have not been reported in white spotted char or bull trout, but Savvaitova (1970, 1973; cited from Armstrong and Morrow 1980) did report discrete piscivorous and benthivorous morphs for Dolly Varden from a large lake in Kamchatka. It is not clear whether these species have less capacity for the trophic specialization observed in Arctic char, or whether this paucity is an artifact of the lack of this type of investigation for these species. At least one study did suggest that some white spotted char may develop dense gill rakers suited to foraging on plankton (Takami and Kinoshita 1990). Certainly the very large lakes with bull trout throughout the central part of that species' range could support ecotypes that have never been recognized because those environments are difficult to sample and research has been focused elsewhere.

Though trophic polymorphisms are not well documented for these species, considerable variation in diet and plasticity in foraging behavior has been observed. Each species has achieved some notoriety for their predatory habitats (Behnke 1980; Takami and Aoyama 1997; Takami and Nagawasa 1996), and all three were actively eradicated in some early management campaigns, with the aim of increasing the early survival of more highly valued anadromous salmonids upon which they prey. However, all three species

exhibit a spectrum of foraging, from strict piscivory (including cannibalism) to a focus on invertebrate prey. Moreover, these char display flexibility in their mode of foraging. For instance, both Dolly Varden and bull trout have been observed to shift from drift-feeding on aquatic and terrestrially-derived invertebrates to picking benthic invertebrates from the substrate in response to diminished supply of drifting prey or competition with other salmonids for this resource (Fausch et al. 1997; Nakano et al. 1992; Nakano et al. 1999). Likewise, all three taxa are known to opportunistically shift to scavenging of fish eggs, especially those of Pacific salmon (e.g., Morton 2004), but also those of con-specifics (Maekawa and Hino 1987).

Movement

A common theme among chars considered here is that they all exhibit a great deal of variation in migratory behavior and related population characteristics. Migration is typically tied to availability of food resources that are distant from natal locations, although the relative benefits of migration may vary between the sexes (e.g., Jonsson and Jonsson 1993). Often, longer distance migrations are associated with entry into seawater, or anadromy. Anadromy is common in whitespotted char and Dolly Varden and is more prevalent at higher latitudes (Yamamoto et al. 1999; *Savvaitova*), consistent with expectations of differential productivity in freshwater and marine environments (Maekawa and Nakano 2002). Anadromy is also known in bull trout (Brenkman et al. in press) though much less common, perhaps because the species' range is more inland in comparison to Dolly Varden and white-spotted char. In addition to availability of food resources, another yet to be tested hypothesis to explain migratory behavior of char is

related to the "egg-fry conflict" (Quinn 2005), and invokes selection of optimal temperatures for growth. Char depend on very cold water for successful egg incubation (e.g., McPhail and Murray 1979), yet these cold habitats are not ideal for juvenile growth (Selong et al. 2001). Thus, it may be advantageous for juveniles to emigrate to find relatively warmer habitats where they are able to grow faster. Both the food availability and temperature likely play a key role in determining the movement and migratory behavior of chars (e.g., Hughes and Grand 2000).

All three char use a wide range of migratory habitats, including larger rivers, lakes, and marine habitats. Limited evidence suggests that within populations showing long-distance (>20 km) migrations, larger (>300 mm) individuals tend to move quickly between natal habitats and migratory destinations, whereas behavior of smaller (<300 mm) migratory individuals is more diverse and less predictable (Muhlfield and Marotz 2005; Monnot et al., in press). Thus, there may be important age or life-stage dependent patterns of migration, and variability in migratory behavior is much more complex than classic definitions based only on origins or destinations of migration. In many cases, the actual "destination" of migration is not clear, as fish may use multiple habitats for extended periods during migration (e.g., Brenkman and Corbett 2005), or change destinations among years, including cases of bull trout switching destinations between major drainage basins (J. Delavergne, U.S. Fish and Wildlife Service, personal communication).

Another less-studied factor influencing migratory behavior is sex. Small resident or so-called "precocious" males have been noted in Dolly Varden (Koizumi), white spotted charr (Morita), and bull trout (Kitano et al. 1994; Baxter 2000). Even in

populations considered to be largely migratory, we would therefore expect to find a significant number of non-migratory males that mature at a small size. This expectation is based on the common occurrence of smaller males adopting "sneaking" mating tactics in many other closely related fishes (e.g., Esteve 2005). The likely occurrence of such individuals is of critical importance, since they are unlikely to be considered in typical counts of adults or spawning surveys. In summary, movement is a defining feature of these chars, and our understanding of movements and migrations have been largely limited to descriptive studies, with only a few examples of hypothesis-driven inquiries into the processes that drive different patterns of movement. More work is needed to explicitly frame movement and migration within a more ecological-evolutionary context (Jonsson and Jonsson 1993), and move beyond simple descriptions of where and when fish move.

Species interactions and ecosystem roles

Biotic interactions may be important in shaping the distribution and abundance of these chars, and reciprocally their distribution sets the stage for their interactions with one another, with other species, and the roles they may play in the ecosystems they inhabit. Char distribution may be affected by the availability of prey species, competition for these or other resources, regulation by predation or parasitism, or additional indirect interactions within their ecosystems. Research on biotic interactions involving these chars has largely focused on their potential competition with other native and nonnative salmonids, whereas relatively little is known about interactions involving these char as predators or prey of native biota, or other roles they may play in ecosystems.

Interspecific competition with native salmonids

Though the ranges of white-spotted char and bull trout overlap with Dolly Varden, they are not often found together at the local scale. In regions where the species overlap, Dolly Varden occur in upstream segments whereas either of the other two species occur downstream, and there is typically a narrow zone of sympatry. For example, in Hokkaido Island this distribution pattern is observed for Dolly Varden and white-spotted char and is correlated with changes in temperature across the region and within basins (Fausch et al. 1994).

Interspecific competition with other native salmonids is considered important in causing exclusion of these chars or regulating coexistence with the other salmonids. For example, in coastal British Columbia lakes, native coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) exclude Dolly Varden from the productive near-shore littoral zone during summer where food resources are richest, causing them to shift to foraging in the open waters or deep benthic zone (Henderson and Northcote 1985, Hindar et al. 1988). In streams, salmonids compete for positions in mixed-species dominance hierarchies from which they can ambush drifting invertebrate prey (Fausch and White 1986, Nakano 1995). However, Dolly Varden are adept at shifting their foraging mode from feeding on this drift to picking benthic invertebrates from the substrate as resources decline throughout summer (Fausch et al. 1997, Nakano et al. 1999). This allows them to partition food resources with white-spotted char in zones where they overlap in Hokkaido mountain streams, and may promote coexistence. However, at the watershed scale, the

exclusion and coexistence of these char is regulated by interactions among competitive dominance and physiological tolerance that change with water temperature (Taniguchi and Nakano 2000). White-spotted char dominate Dolly Varden in both behavior and growth at warmer temperatures in downstream reaches, but are limited physiologically by cold temperatures in upstream reaches where Dolly Varden can persist.

Interactions with nonnative salmonids

In contrast to interactions with native salmonids that shape char distribution, the introduction and invasion of nonnative salmonids has threatened to extirpate these three chars from much habitat throughout broad regions of their distribution via hybridization, competition, and disrupting spawning (Fausch 1988, Dunham et al. 2002, Kitano 2004). Introgressive hybridization with brook trout has been reported for bull trout in northwestern North America (Leary et al. 1993) and for white-spotted char in Honshu and Hokkaido islands in Japan (Suzuki and Kato 1966, Kitano 2004, Kitano, unpublished data), and may result in displacement of the native char. However, in both cases most F1 hybrids are almost sterile, which may limit the spread of this hybrid swarm (Allendorf et al. 2001). With respect to interspecific competition, brook trout have invaded throughout the western U.S., and were reported to exclude resident bull trout from favorable foraging microhabitats in a Montana stream (Nakano et al. 1998). Likewise, rainbow trout and brown trout are rapidly invading Hokkaido Island (Takami and Aoyama 1999, Takami et al. 2002), and exclude Dolly Varden and white-spotted char from foraging positions or habitats in Hokkaido streams (Baxter et al. 2004, Morita et al. 2004, Hasegawa et al. 2004, Hasegawa and Maekawa 2005). In a field experiment, rainbow trout usurped

terrestrial invertebrate prey on which Dolly Varden depend, and reduced their growth by 35% in six weeks compared to control reaches (Baxter et al. 2007). In addition, spring spawning rainbow trout can reduce reproductive success of native fall-spawning char by digging up their spawning redds before the fry emerge (termed superimposition; Taniguchi et al. 2000). Moreover, comparative evidence indicates that lake trout introduced into lakes in western North America have displaced bull trout, but the mechanisms are unclear (Fredenberg 2002).

Despite this evidence for displacement, in other cases several of these salmonids appear to coexist with the char where their native ranges overlap. For example, Dolly Varden coexist with rainbow trout or steelhead (*O.* mykiss) in Alaska watersheds, probably by partitioning food resources via the foraging mode shift described above (see Dollof and Reeves 1990, Fausch et al. 1997). Lake trout and bull trout coexist in certain lakes in western North America (Donald and Alger 1993) and rainbow trout and bull trout coexist in watersheds in the same region, apparently through coevolved mechanisms, but these have not yet been studied. However, an important hypothesis is that the native char can resist invasion and persist in watersheds where intact habitat allows maintaining the full range of life history forms, including large migratory char that are highly fecund. When habitat is fragmented or degraded, and these migratory forms are lost through habitat loss or overfishing, biologists report that invasions are more likely to displace the native char (B. R. Rieman and K. Morita, personal observation). Thus, understanding the mechanisms that promote or resist invasions by nonnative species (and the interactions of these mechanisms with habitat fragmentation) is among the most important topics for future research.

Ecosystem roles

Relatively little is known about interactions involving these chars as predators or prey of native biota, or other roles they may play in ecosystems. Bull trout are strong predators on *Oncorhynchus* spp. (*O. nerka* and *O. mykiss*) and con-specifics in lakes in the inland western U.S., where they become more piscivorous with increasing size (Ricker 1941, Beauchamp and Van Tassell 2001). During periods of spawning by Pacific salmon or when young salmon are concentrated during the out-migration of smolts, salmon eggs or juveniles may become a temporarily important food for anadromous populations of Dolly Varden and white-spotted char (Armstrong and Morrow 1980, Kawanabe and Mizuno 1989, Morton 2004). Char are, in turn, known to be hosts for some invertebrates, virus, bacteria and fungi (Armstrong and Morrow 1980, Nagasawa 1989). In addition to their role as prey for conspecifics and other piscivorous fishes, these chars may be food for a host of semi-aquatic and terrestrial predators such as otters, bears, birds, or snakes, though we are aware of no focused study of these interactions.

Dolly Varden, white-spotted char, and bull trout likely have important affects on the structure of communities and the flow of energy and nutrients in the ecosystems they inhabit, though there have been almost no investigations of this topic. Through their roles as predators on invertebrates and other fishes these chars have the capacity to indirectly regulate organisms at lower trophic levels. For instance, two studies conducted in northern Japan (Nakano et al. 1999, Baxter et al. 2004) showed that when terrestrial invertebrate prey were experimentally reduced, Dolly Varden intensified their foraging on benthic invertebrates, which triggered an increase in the growth of algae but also

reduced the emergence of adult aquatic insects and the abundance of spiders in the riparian forest. Though limited in their scope, these results suggest that Dolly Varden may regulate algal abundance and even affect terrestrial predators when prey other than stream invertebrates are not available. Studies like these have not been conducted for bull trout or white-spotted char, but similar indirect effects on algae have been described for brook trout in a Canadian stream (Bechara et al. 1992). If predation by these chars can regulate prey fish populations in lakes, they could indirectly control phytoplankton dynamics, as has been described for many other piscivorous fishes, including lake trout and Arctic char (Carpenter and Kitchell 1993). Moreover, through their migratory life histories these chars can play roles yet to be described that link the food webs of multiple habitats and may also transport energy and nutrients as has been found for other migratory fishes (e.g., Gende et al. 2002, Polis et al. 2004).

Shared challenges for conservation

Many of the conservation problems for Dolly Varden, white-spotted char, and bull trout can be understood within the traditional province of examining threats that have likely contributed to declines of populations. Newer tools from conservation biology, such as population viability analysis (Beissinger and McCullough 2002), analyses of species occurrence (Dunham et al. 2002), and conservation and landscape genetics (Neville et al. 2006) have also been applied. Ultimately, insights from both traditional and newer approaches have provided a much richer understanding of factors contributing to the persistence and long-term viability of these chars (Caughley 1994).

Population viability analysis has been applied to assess long-term persistence of bull trout and white-spotted char (Rieman and McIntyre 1993; Morita and Yokota 2002; Post et al. 2003). In both species, sensitivity analyses have pointed to the importance of survival of older age classes to population persistence. Post et al. (2003) found populations of migratory bull trout may be highly susceptible to declines from increased mortality of larger, older fish due to angling. Bull trout (especially females) in such systems do not attain first maturity with a high likelihood until at least 5 years of age. Morita and Yokota (2002) similarly found that survival of adults was important for population persistence of white-spotted char in highly fragmented river systems. In their system, however, white-spotted char matured at much smaller sizes and ages (e.g., most females were mature by age 2). Thus in both migratory bull trout and non-migratory white-spotted char, survival of adults appears to be a critical factor influencing population persistence. Morita and Yokota (2002) also found that increased carrying capacity had a substantial influence on local population persistence, as may be expected. An important implication was that many smaller and isolated populations of white-spotted char were likely to become extinct in the future, a result confirmed by an empirical analysis of the effects of habitat size and time since isolation on population persistence (Morita and Yamamoto 2002). In addition to providing perspectives on population persistence and threats to local populations, population viability analysis may be useful for understanding population trends, which has proven difficult in retrospective analyses of population time series (Maxell 2000). A new approach based on simulation of population trajectories (= future trends) with existing demographic data may provide a better alternative (Staples et al. 2005). This approach is similar to population viability

analysis, and uses information on current population time series to project and assess possible future trends, rather than assessment of past trends.

Whereas population viability analysis has provided important perspectives on the dynamics of individual populations of native char, in most cases they are embedded within a network of habitats and other populations. At this scale, connectivity among populations (dispersal) and migrations among habitats used for feeding, breeding, or refuge (Schlosser 1991) are relevant. It is most likely that aggregations of local salmonine populations exhibit complex dynamics and structuring that represents a composite of different metapopulation, landscape, and historical processes (Neville et al., 2006; Koizumi et al. 2006; Whiteley et al. 2007). Because many of these processes can operate on large (>10 km) spatial and long (>10 year) temporal scales, they are very difficult to study with conventional ecological methods. Single "snapshot" studies of large scale patterns of habitat or "patch" occupancy by bull trout (Dunham and Rieman 1999), white-spotted char (Morita and Yamamoto 2002), and Dolly Varden char (Koizumi and Maekawa 2004) show that local population persistence in stream networks is strongly tied to patch size (stream or watershed size), connectivity, and quality (e.g., human influences, flow regime). The importance of habitat size and connectivity to persistence of chars from these "snapshot" studies is supported by inferences about temporal processes (e.g., dispersal, demographic variation, environmental variability) driving these patterns. First, simulated population dynamics have provided supportive results concerning habitat size, if it can be assumed that larger habitats support larger populations (Morita and Yokota 2002) and the importance of dispersal among habitats (Rieman and Allendorf 2001). Empirical applications of molecular genetic markers also

provide a basis for indirectly inferring dispersal among populations and the effective sizes of local populations (Neville et al. 2006). Results from work on native chars show that disruption of connectivity can lead to lower effective size of local populations by simultaneously reducing dispersal and local adult population sizes (Griswold 2002; Costello et al. 2003; Yamamoto et al. 2004; Whiteley et al. 2007; Koizumi et al. 2006; Yamamoto et al. 2006).

Our understanding of the dynamics of single and networked populations of native chars is far from complete, but much has been learned. In contrast, for the species considered herein, much less is known about the question of reserve design. Dolly Varden, white-spotted char, and bull trout show a general south to north trend in the status of populations. This is perhaps not surprising, given the dependence of these species on cold, clean, freshwaters, and the corresponding distribution of human populations. For all species, population persistence at southern range margins for each species has been tied to the presence of cold, constant flows provided by groundwater (Goetz 1989; Nakano et al. 1996; Koizumi and Maekawa 2004). Cold water is a major necessary, but insufficient condition for populations to persist, as demonstrated by evidence cited above showing populations to be more likely to occur or persist in larger "patches" of cold water. Thus, in addition to local habitat quality (e.g., cold water temperatures), the spatial structure of habitat is critical. Concern over changes to river thermal regimes resulting from the direct or indirect effects of climate change has been repeatedly raised for these species (Nakano et al. 1996; Rieman et al. 1997; Rieman et al., unpublished).

In addition to climate change, rapid growth of human populations at the southern margins of the ranges for Dolly Varden, white spotted char, and bull trout has placed tremendous pressures on water resources, often leading to habitat loss and degradation, invasion of nonnative species, excessive harvest (legal, poaching, and incidental mortality; Post et al. 2003), and other influences that have driven populations to extinction in just a few decades, such as introductions of nonnative salmonids (see *Interactions with nonnative salmonids*, above). As considered here, reserve design is focused on identifying strategies for long-term conservation of the ecological and evolutionary diversity within a species (Groves 2003). Natural diversity within and among char populations is well-documented, including genetic, and life history diversity, as well as diversity in the range of habitats they use (see above). Understanding these patterns and contributing processes provides the foundation for designing reserves. The high levels of phenotypic and evolutionary diversity observed in the chars considered here (and characteristic of all salmonines) likely reflect influences from the diverse environments they evolved in.

In most of Russia and parts of the northern US and Canada, chars largely exist in pristine environments, with few contemporary influences of humans. Further to the south in Canada, the United States, and Japan, protected areas that support current strongholds of native chars are a biased sample of the full range of habitats that were historically occupied. For example, in the United States, many strongholds for bull trout are located in higher elevation wilderness areas, whereas historically occupied areas were much more expansive (Rieman et al. 1997). Lower elevation habitats such as floodplains of large rivers are critical to many salmonines, but they are also most likely to be highly altered

by humans (Beechie et al. 2003). A focus on protecting only existing populations of native chars may therefore risk ignoring locations and/or habitats that are just as, if not more important for long-term viability. Furthermore, it is unlikely that many current strongholds will persist indefinitely, whether in human dominated or pristine environments. It is more likely that conditions will change substantially across landscapes in response to cycles of natural disturbance and succession processes (Reeves et al. 1995; Dunham et al. 2003). The past dynamics of habitats and populations may not represent the future, especially in light of climate change (Nakano et al. 1996) and localized human influences, such as introductions of nonnative species. Thus, reserve design needs to consider not only the present ecological and evolutionary historical context for a species, but also conditions that will likely prevail into the future. Many case studies suggest that even large populations can become highly vulnerable if present conditions change. For example, bull trout were once very abundant in the Flathead River system in western Montana, but populations quickly crashed in the early 1990s due to major ecosystem changes caused by the introduction of nonnative species, including lake trout (*Salvelinus namaycush*) and opossum shrimp (*Mysis relicta*) (Spencer et al. 1991). We view threats analysis and reserve design to be among the highest priority information needs for understanding long-term conservation of the native chars considered here.

Conclusions

Until recently, Dolly Varden, white-spotted char, and bull trout shared a common history of being reviled by anglers and fishery managers alike, largely due to their perceived negative effects on more valued fisheries, such as those for salmon and trout (*Oncorhynchus*, spp.). Social perceptions are gradually becoming more positive as the imperiled status of populations in many areas has attracted increasing interest from government agencies and conservation groups. As more is learned about these unique species, appreciation of them grows. From what we have learned it is clear these chars depend strongly on large, intact stream networks with an abundant supply of cold, clean freshwater. They are often denizens of the most remote and less trammeled watersheds. Like the chars themselves, these are increasingly short in supply.

While much remains to be learned of the evolution and ecology of these species, we hope to learn more about them in their natural conditions, rather than through what happens as their populations and habitats are lost. In most places where these species live, very little is known, and many populations remain to be discovered or properly described. It is also likely that past extinctions have occurred before populations were known to fishery managers. Experience in fishery management has shown clearly that preventing problems is much more effective than restoring lost populations or habitat conditions, and there are many such opportunities for Dolly Varden, white spotted char, and bull trout. But efforts for protection cannot be done in a vacuum. Because these species occupy broad and overlapping ranges across the Pacific Rim, spanning the boundaries of >3 countries for each alone, we encourage a stronger internationally-based approach to their long-term protection and conservation for future generations.

Literature Cited

Allendorf, F. W., R. F. Leary, P. Spruell, and J. K. Wenburg. 2001. The problems with hybrids: setting conservation guidelines. Trends in Ecology and Evolution 16: 613-622.

Armstrong, R. H., and J. E. Morrow. 1980. The Dolly Varden charr, *Salvelinus malma*. Pages 99-140 in E.K. Balon, ed. Charrs: salmonid fishes of the genus *Salvelinus*. Dr. W. Junk -bv, Publishers, The Hague, Netherlands.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream forest food webs by interrupting reciprocal prey subsidies. Ecology 85:2656-2663.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2007. Invading rainbow trout usurp a terrestrial prey subsidy to native charr and alter their behavior, growth, and abundance. Oecologiε

Beauchamp, D. A. and J. J. Van Tassell. 2001. Modeling seasonal trophic interactions of adfluvial bull t in lake Billy Chinook, Oregon. Transactions of the American Fisheries Society 130: 204-216.

Bechara, J. A., G. Moreau, and D. Planas. 1992. Top-down effects of brook trout (Salvelinus fontinalis) boreal forest stream. Canadian Journal of Fisheries and Aquatic Sciences 49:2093-2103.

Beechie, T. J., P. Roni, E.A. Steel, and E. Quimby, editors. 2003. Ecosystem recovery planning for liste salmon: An integrated assessment approach for salmon habitat. Seattle, Washington: U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Technical Memorandum, NMFS-NWFSC-58.

Behnke, R.J. 1980. A systematic review of the genus *Salvelinus*. Pages 441-480 In Balon, E.K. (editor) Charrs: salmonid fishes of the genus salvelinus, W.Junk Publ., The Hague, Netherlands

Beissinger, S. R., and D. R. McCullough, ed. 2002. Population viability analysis. Chicago, Illinois: University of Chicago Press.

Brenkman, S. J., and S. C. Corbett. 2005. Extent of anadromy in bull trout and implications for conserva of a threatened species. North American Journal of Fisheries Management. 25:1073-1081.

Brenkman et al. In press

Brunner, P. C., M. R. Douglas, A. Osinov, C. C. Wilson, L. Bernatchez. 2001. Holarctic phylogeograph arctic charr (*Salvelinus alpinus* L.) inferred from mitochondrial DNA sequences. Evolution 55: 5 586.

Carpenter and Kitchell 1993

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63: 215-244.

Cavender, T.M. 1978. Taxonomy and distribution of the bull trout, *Salvelinus confluentus* (Suckley), fro the American Northwest. California Fish and Game 3:139-174.

Costello, A. B., T. E. Down, S. M. Pollard, C. J. Pacas, and E. B. Taylor. 2003. The influence of history contemporary stream hydrology on the evolution of genetic diversity within species: an examina of microsatellite DNA variation in bull trout, *Salvelinus confluentus* (Pisces: Salmonidae). Evolu 57:328-344.

Crane et al. 1994

Crespi, B. J., and M. J. Fulton. 2003. Molecular systematics of salmonidae: combined nuclear data yield robust phylogeny. Molecular Phylogenetics and Evolution 31: 658-679.

Dolloff and Reeves 1999

Donald, D. B. and Alger, D. J. 1993. Geographic distribution, species displacement, and niche overlap f lake trout and bull trout in mountain lakes. Canadian Journal of Zoology 71:238-247.

Dunham, J. B., and Rieman, B. E., 1999. Metapopulation structure of bull trout: influences of physical, biotic, and geometrical landscape characteristics. Ecological Applications 9:642-655

Dunham, J. B., S. B. Adams, R. E. Schroeter, and D. C. Novinger. 2002a. Alien invasions in aquatic ecosystems: toward an understanding of brook trout invasions and their potential impacts on inla cutthroat trout in western North America. Reviews in Fish Biology and Fisheries 12:373-391.

Dunham, J.B., B.E. Rieman, and J.T. Peterson. 2002b. Patch-based models of species occurrence: lessor from salmonid fishes in streams. Pages 327-334 in Scott, J.M., Heglund, P. J., Morrison, M., Raphael, M., Haufler, J. and Wall B. (editors). Predicting species occurrences: issues of scale and accuracy. Island Press. Covelo, CA.

Dunham, J.B., M.K. Young, R.E. Gresswell, and B.E. Rieman. 2003. Effects of fire on fish populations: landscape perspectives on persistence of native fishes and non-native fish invasions. Forest Ecolo and Management 178:183-196.

Esteve, M. 2005. Observations of spawning behaviour in Salmoninae: *Salmo*, *Oncorhynchus* and *Salveli* Reviews in Fish Biology and Fisheries 15: 1–21.

Fausch, K. D. 1988. Tests of competition between native and introduced salmonids in streams: What ha we learned? Canadian Journal of Fisheries and Aquatic Science 45: 2238-2246.

Fausch, K. D., S. Nakano, and K. Ishigaki. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. Oecologia 100: 1-12.

Fausch, K. D., S. Nakano, and S. Kitano. 1997. Experimentally induced foraging mode shift by sympatr charrs in a Japanese mountain stream. Behavioral Ecology 8: 414-420.

Fredenberg, W. 2002. Further evidence that lake trout displace bull trout in Montana lakes. International Journal of Sciences 8: 143-152.

Gende, S. M., E. D. Edwards, M. F. Willson, and M. S. Wipfli. 2002. Pacific salmon in aquatic and terrestrial ecosystems. BioScience 52:917-928.

Goetz, F. 1989. Biology of the bull trout *Salvelinus confluentus*: a literature review. Willamette Na Forest. Eugene, Oregon. 53 pages.

Griswold, K. E. 2002. Genetic diversity in coastal cutthroat trout and Dolly Varden in Prince William Sound, Alaska. Doctoral Dissertation. Oregon State University, Corvallis, OR.

Groves, C. 2003. Drafting a conservation blueprint. Covelo, California: Island Press.

Haas, G. R., and J. D. McPhail. 1991. Systematics and distribution of Dolly Varden and bull trout in No America. Canadian Journal of Fisheries and Aquatic Sciences 48: 2191-2211.

Hasegawa K. and K. Maekawa. 2005. Effect of introduced salmonids on two native stream-dwelling salmonids through interspecific competition. Jounal of Fish Biology 68:1123-1132.

Hasegawa K., T. Yamamoto, M. Murakami, and K. Maekawa. 2004. Comparison of competitive ability between native and introduced salmonids: evidence from pairwise contests. Ichthyological Resea 51: 191-194.

Henderson, M. A. and T. G. Northcote. 1985. Visual prey detection and foraging in sympatric cutthroat trout (*Salmo clarki clarki*) and Dolly Varden (*Salvelinus malma*). Canadian Journal of Fisheries a Aquatic Sciences 42: 785

Hindar, K., B. Jonsson, J. H. Andrew, and T. G. Northcote. 1988. Resource utilization of sympatric and experimentally allopatric cutthroat trout and Dolly Varden charr. Oecologia 74: 481-491.

Hughes and Grand 2000

Jonsson, B., and N. Jonsson. 1993. Partial migration - niche shift versus sexual-maturation in fishes. Reviews in Fish Biology and Fisheries 3:348-365.

Jonsson, B, S. Skulason, Snorrason, O. T. Sandlund, H.J. Malmquist, P. M. Jonasson, R. Gydemo, and T Lindem. 1988. Life history variation of polymorphic arctic charr (*Salvelinus alpinus*) in Thinvallavatin, Iceland. Canadian Journal of Fisheries and Aquatic Sciences. 45:1537-1547.

Kawanabe, H. 1989. Japanese char(r(r))s and masu-salmon problems: a review. Physiology and Ecology Japan, Special volume 1: 13-24.
Kawanabe, H. and N. Mizuno (eds.) 1989. Freshwater fishes of Japan. Yamakei Publishers. Tokyo (In Japanese).
Kitano, S. 2004. Ecological Impacts of Rainbow, Brown and Brook Trout in Japanese Inland Waters. Global Environmental Research 8: 41-50.
Kitano, S., K. Maekawa, S. Nakano, and K. D. Fausch. 1994. Spawning behavior of bull trout in the upp Flathead River drainage, Montana, with special reference to hybridization with brook trout. Transactions of the American Fisheries Society 123:988-992.
Koizumi, I., & Maekawa, K. 2004. Metapopulation structure of stream-dwelling Dolly Varden charr inferred from patterns of occurrence in the Sorachi River basin, Hokkaido, Japan. Freshwater Bio 49: 973 – 981.
Leary, R. F., F. W. Allendorf and S. H. Forbes. 1993. Conservation genetics of bull trout in the Columbi and Klamath River drainages. Conservation Biology 7: 856-865.
Maekawa, K. 1984. Life history patterns of the Miyabe charr in Shikaribetsu Lake, Japan. Pages 233-25 L. Johnson, and B. L. Burns, editors. Biology of the Arctic Charr, Proceedings of the Internationa Symposium on Arctic Charr. University of Manitoba Press, Winnipeg.
Maekawa, K., and T. Hino. 1987. Effect of cannibalism on alternative life histories in charr. Evolution 41:1120-1123.
Maxell, B. A. 1999. A power analysis on the monitoring of bull trout stocks using redd counts. North American Journal of Fisheries Management 19:860-866.
McPhail, J. D., and C. B. Murray. 1979. The early life history and ecology of Dolly Varden (Salvelinus malma) in the Upper Arrow Lakes. British Columbia Hydro and Power Authority and Kootenay Region Fish and Wildlife, Vancouver, B.C.
Monnot, L., J.B. Dunham, T. Hoem, and P. Koetsier. In press. Influences of body size and environmenta factors on autumn downstream migration of bull trout in the Boise River, Idaho. North American Journal of Fisheries Management.
Morita, K., and S. Yamamoto. 2002. Effect of habitat fragmentation by damming on the persistence of stream dwelling charr populations. Conservation Biology. 16:1318-1323.
Morita and Yokota 2002
Morita K., J. I. Tsuboi, and H. Matsuda. 2004. The impact of exotic trout on native charr in a Japanese stream. Journal of Applied Ecology, 41: 962-997.
Muhlfeld, C.C. and B. Marotz. 2005. Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. North American Journal of Fisheries Management 25: 7 810.
Nagasawa, K. 1989. Microbial and fungal diseases in masu and charr cultured in Japan: a review. Physiology and Ecology Japan, Special volume 1: 547-558.
Nakano, S. 1995. Competitive interactions for foraging microhabitats in a size-structured interspecific dominance hierarchy of two sympatric stream salmonids in a natural habitat. Canadian Journal of Zoology 73: 1845-1854.
Nakano, S., K. D. Fausch, T. Furukawa-Tanaka, K. Maekawa, and H. Kawanabe. 1992. Resource utiliza by bull char and cutthroat trout in a mountain stream in Montana, U.S.A. Japanese Journal of Ichthyology 39:211-216.
Nakano, S., F. Kitano, and K. Maekawa. 1996. Potential fragmentation and loss of thermal habitats for charrs in the Japanese archipelago due to climatic warming. Freshwater Biology 36:711-722.

Nakano, S., S. Kitano, K. Nakai, and K. D. Fausch. 1998. Competitive interactions for foraging microhabitat among introduced brook charr, *Salvelinus fontinalis*, and native *S. confluentus*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in a Montana stream. Environmental Biolo of Fishes 52: 345-355.

Nakano, S., K. D. Fausch, and S. Kitano. 1999. Flexible niche partitioning via a foraging mode shift: a proposed mechanism for coexistence in stream-dwelling charrs. Journal of Animal Ecology 68: 1079-1092.

Neville, H.N., J.B. Dunham, and M.M. Peacock. Assessing connectivity in salmonid fishes with DNA microsatellite markers. Pages 318-342 *in* K. Crooks and M.A. Sanjayan, editors. Connectivity conservation: maintaining connections in nature, Cambridge University Press.

Oleinik, A. G., L. A. Skurikhina, VI. A. Brykov, P. A. Crane, J. K. Wenburg. 2005. Differentiation of D Varden char *Salvelinus malma* from Asia and north America inferred from PCR-RFLP analysis o mitochondrial DNA. Russian Journal of Genetics 41: 501-508.

Phillips, R. B., L. I. Gudex, K. M. Westrich, A. L. DeCicco. 1999. Combined phylogenetic analysis of ribosomal ITS1 sequences and new chromosome data supports three subgroups of Dolly Varden ((*Salvelinus malma*). Canadian Journal of Fisheries and Aquatic Sciences 56: 1504-1511.

Polis, G. A., M. E. Power, and G. R. Huxel. 2004. Food webs at the landscape level. University of Chica Press, Chicago.

Quinn, TP. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Pre Seattle, WA.

Radchenko, O. A. 2004. Introgressive hybridization of chars of the genus *Salvelinus* as inferred from mitochondrial DNA variation. Russian Journal of Genetics 40: 1678-1685.

Reeves, G.H., Benda, L.E., Burnett, K.M., Bisson, P.A. & Sedell, J.R. 1995. A disturbance-based eco approach to maintaining and restoring freshwater habitats of evolutionarily significant units o anadromous salmonids in the Pacific Northwest. In: Nielsen, J.L. ed. Evolution and the aquatic ecosystem: defining unique units in population conservation. American Fisheries Society Sympos 17. Bethesda, Maryland, pp. 334-349.

Ricker, W. E. (1941) The consumption of young sockeye salmon by predaceous fish. Journal of the Fisheries Research Board of Canada 5:293-313.

Rieman, B.E. and FW. Allendorf. 2001. Effective population size and genetic conservation criteria for trout. North American Journal of Fisheries Management 21:756-764.

Rieman, B.E. and J.D. McIntyre. 1993. Demographic and habitat requirements for the conservation of bu trout *Salvelinus confluentus*. USDA Forest Service Intermountain Research Station, General Technical Report INT-302, Ogden, UT.

Rieman, B.E., Lee, D.C. and Thurow, R.F. 1997. Distribution, status, and likely future trends of bull tro within the Columbia River and Klamath basins. North American Journal of Fisheries Manageme 17: 1111-1125.

Savvaitova, K. A. 1980. Taxonomy and biogeography of charrs in the Palearctic. Pages 281-294 in E. K Balon, ed. Charrs: salmonid fishes of the genus Salvelinus. Dr. W. Junk -bv, Publishers, The Hag Netherlands.

Schlosser, I.J. 1991. Stream fish ecology: a landscape perspective. BioScience. 41: 704-712.

Selong, J.H., T.E. McMahon, A.V. Zale and F.T. Barrows. 2001. Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerance i fishes. Transactions of the American Fisheries Society. 130: 1026-1037.

Smith, T. B., and S. Skúlason. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. Annual Review of Ecology and Systematics 27:111-133.

Spruell, P., A. R. Hemmingsen, P. J. Howell, N. Kanda, and F. W. Allendorf. 2003. Conservation geneti of bull trout: geographic distribution of variation at microsatellite loci. Conservation Genetics 4: 29.

Spencer, C. N., B. R. McClelland, and J. A. Stanford. 1991. Shrimp stocking, salmon collapse, and eagl displacemnent: cascading interactions in the food web of a large aquatic ecosystem. BioScience 41:14-21.

Suzuki, R. and T. Kato. 1966. Hybridization in nature between salmonid fishes, *Salvelinus pluvius* x *Salvelinus fontinalis*. Bulletin of the Freshwater Fisheries Research Laboratory, 17: 83-90.

Takami, T., and T. Aoyama.1999. Distributions of rainbow trout and brown trouts in Hokkaido, northern Japan. Wildlife Conservation Japan 4: 41-48. (In Japanese with English Abstract)

Takami, T., and Kinoshita, T. 1990. Morphological comparisons of charr, *Salvelinus leucomaenis* (Palla obtained from Lake Shikotsu and Moheji River in Hokkaido, Japan. Bulletin of the Faculty of Fisheries, Hokkaido University. 44: 121-130.

Takami, T., and Nagawasa, K. 1996. Predation on chum salmon (*Oncorhynchus keta*) fry and masu salm (*O. masou*) juveniles by white-spotted charr (*Salvelinus leucomaenis*) in a river in northern Japan Scientific Reports of the Hokkaido Fish Hatchery, 50: 45–47.

Takami, T., T. Yoshihara, Y. Miyakoshi, and R. Kuwabara. 2002. Replacement of the white-spotted cha *Salvelinus leucomaenis* by brown trout *Salmo trutta* in a branch of the Chitose River, Hokkaido. Nippon Suisan Gakkaishi, 68: 24-28. (In Japanese with English Abstract)

Taniguchi, Y., and S. Nakano. 2000. Condition-specific competition: implications for the altitudinal distribution of stream fishes. Ecology. 81: 2027-2039.

Taniguchi, Y., Y. Miyake, T. Saito, H. Urabe, and S. Nakano. 2000. Redd superimposition by introduce rainbow trout on native charrs in a Japanese stream. Ichthyological Research 47: 149-156.

Taylor, E. B. 2004. Evolution in mixed company, Evolutionary inferences from studies of natural hybridization in salmonidae. Pages 232-263 in A. P. Hendry and S. C. Stearns, editors. Evolution Illuminated: salmon and their relatives. Oxford University Press, Oxford.

Yamamoto, S., K. Morita, and A. Goto. 1999. Geographic variations in life-history characteristics of wh spotted charr (Salvelinus leucomaenis). Canadian Journal of Zoology 77, 871-878.

Yamamoto, S., K. Morita, S. Kitano, K. Watanabe, I. Koizumi, K. Maekawa, and K. Takamura. 2004. Phylogeography of white-spotted charr (*Salvelinus leucomaenis*) inferred from mitochondrial DN sequences. Zoological Science 21: 229-240.

Yamamoto, S., S. Kitano, K. Maekawa, I. Koizumi, and K. Morita. 2006a. Introgressive hybridization between Dolly Varden *Salvelinus malma* and white-spotted charr *Salvelinus leucomaenis* on Hokkaido Island, Japan. Journal of Fish Biology 68 (Supplement A): 68-85.

Figure Legends

Figure 1. Distributions of Dolly Varden, white-spotted char, and bull trout around the North Pacific rim.

Figure 2. Photos showing four subspecies of Dolly Varden: a) the northern Dolly Varden *S. malma malma* (Walbaum), b) the southern Asian Dolly Varden *S. m. krascheninnikovi* (Taranetz), c) the southern American Dolly Varden *S. m. lordi* (Günther), and d) the Miyabe char *S. m. miyabei* (Oshima).

Figure 3. Photos showing four subspecies of white-spotted char: *S. leucomaenis leucomaenis* (Pallas), *S. l. japonicus* (Oshima), *S. l. pluvius* (Hilgendorf), and *S. l. imbrius* (Jordan et McGregor).

Figure 4. Photos depicting life history and morphological variation of bull trout: a) large, migratory adult bull trout, b) bull trout from inland stream, c) bull trout from coastal stream.

Figure 1.

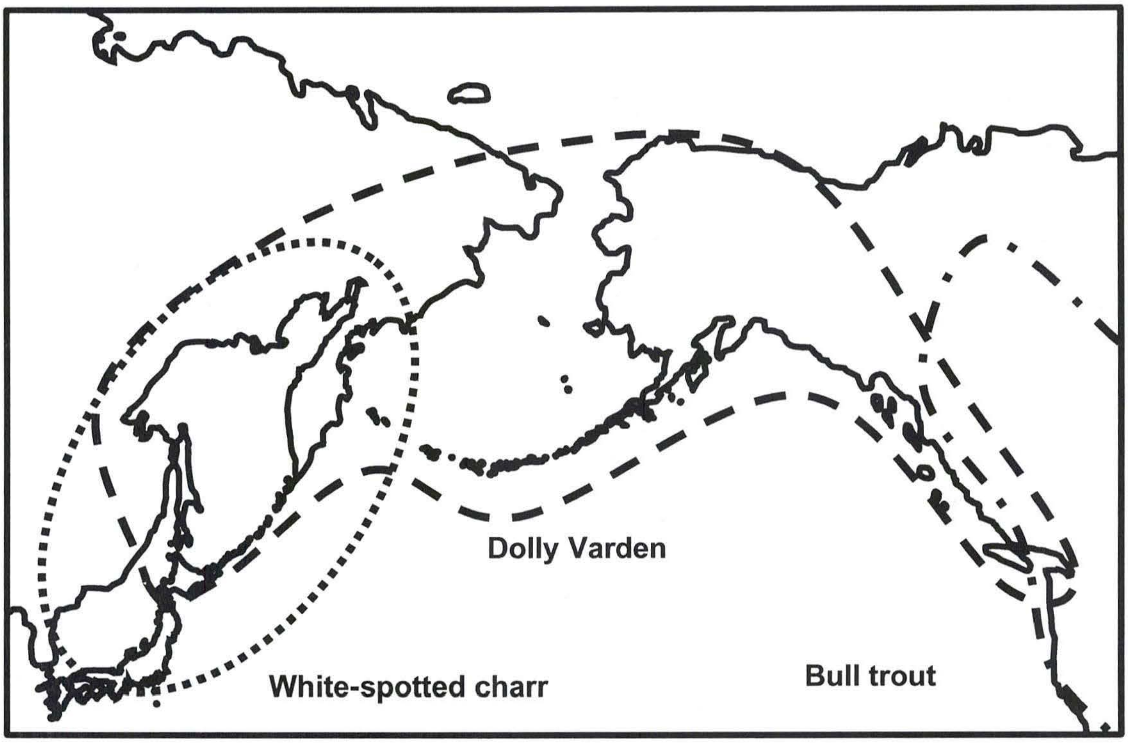
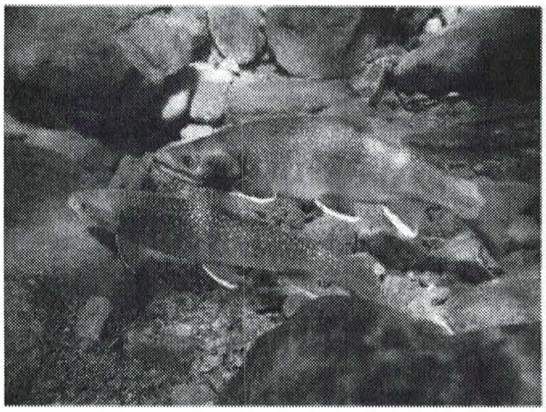


Figure 2.

Salvelinus malma miyabei ***Salvelinus malma krascheninnikovi***



Salvelinus malma malma ***Salvelinus malma lordi***

Figure 3.

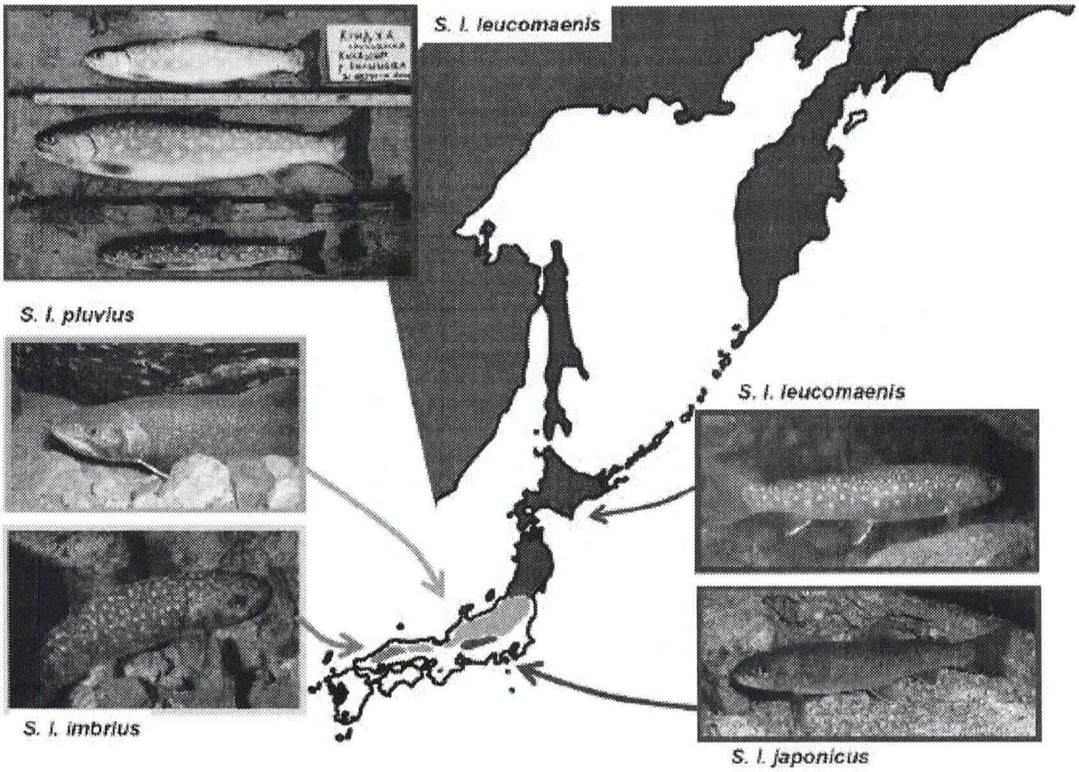

S. l. leucomaenis
S. l. pluvius
S. l. leucomaenis
S. l. imbrius
S. l. japonicus

Figure 4.